SEED AND CAPSULE CHARACTERS IN *ARCYTOPHYLLUM*, *BOUVARDIA*, AND *MANETTIA* (RUBIACEAE), WITH NOTES ON *A. SERPYLLACEUM*

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ABSTRACT

Seed and capsule characters of several species of *Arcytophyllum*, *Bouvardia*, and *Manettia* (Hedyotideae: Rubiaceae) are described and compared. Seed characters are illustrated by scanning electron microscopy. Morphological similarities and differences are emphasized and outlined by a descriptive key. All characters of *Arcytophyllum serpyllaceum* and *A. muticum* were compared in tabular format, and a strong similarity was noted. These results support previous work that considered *A. serpyllaceum* a member of the genus *Arcytophyllum*.

RESUMEN

Las semillas y frutos de algunas especies de *Arcytophyllum*, *Bouvardia* y *Manettia* (Hedyotideae; Rubiaceae) son descritas y comparadas. Los caracteres de las semillas son representados mediante imágenes producidas por un microscopio electrónico de barrido. Las semejanzas y diferencias morfológicas de estos géneros son enfatizadas y esquematizadas por medio de una clave descriptiva. Todos los caracteres de *Arcytophyllum serpyllaceum* y *A. muticum* fueron comparados en una tabla, mostrando éstos un alto grado de similitud. Los resultados obtenidos, apoyan la noción sugerida por estudios previos, de que *Arcytophyllum serpyllaceum* es en realidad un miembro del genero *Arcytophyllum*.

INTRODUCTION

This study of seeds and capsules of three genera belonging to the tribe Hedyotideae (Rubiaceae), follows the pattern of recent work on this tribe (e.g., Terrell 1996; Terrell & Robinson 2003). These studies involved examination of surface features of seeds by dissecting microscope and scanning electron microscopy (SEM). Revision of *Houstonia* (Terrell 1996) showed seed characters and chromosome numbers to be especially important in revealing relationships.

The three genera in the present study, *Arcytophyllum*, *Bouvardia*, and *Manettia*, are from Mexico, and Central and South America. These genera have largely escaped the past tendency to include many members of the tribe in a broad concept of the genus *Hedyotis*, and *Bouvardia* and *Manettia* have sometimes been placed in the tribe Cinchoneae because of the conspicuous papery winged seeds.

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Bremer and Manen (2000) in a molecular study placed *Manettia* and *Bouvardia* in the combined Hedyotideae/Spermacoceae where the older name Spermacoceae was adopted. Terrell and Wunderlin (2003) questioned this action on the basis of fundamental morphological differences between the two tribes. Here and elsewhere (e.g., Terrell & Robinson 2003) we continue to place the present genera in the tribe Hedyotideae sens. str.

All three of our studied genera have recorded chromosome numbers of $x = 9$ (Lewis 1965: 199), a number that is frequent in the Hedyotideae, but unusual in the family Rubiaceae that has mostly $x = 11$.

The purpose of this study is to present for comparison illustrations and/or data on the seeds and capsules of the three genera and to re-examine seed data published by Terrell (1999) and Andersson et al. (2002) for *Bouvardia* and *Arcytophyllum serpyllaceum*.

MATERIALS AND METHODS

Seeds were obtained from the U.S. National Herbarium (US), Smithsonian Institution, and from other herbaria including CHAPA, GH, NY, TENN. Seeds were examined by dissecting microscope and mature, well-formed seeds were viewed by scanning electron microscopy (SEM) at the Smithsonian Institution, and prior to 1985 at the Electronics Lab, U.S. Department of Agriculture, Beltsville, Maryland.

Seed descriptions for each species and inclusive descriptions for each species-group provide basic data.The nomenclatural authors and collection data are added to the seed descriptions for each species. Seed collections viewed by SEM are indicated by a designation such as B35, as e.g. for *Arcytophyllum lavarum*.

Light microscopy was used to observe pollen and some additional structures such as corollas, calyx lobes, and stipules in type species and other selected species of all three genera. Material was mounted on slides in Hoyer's solution (Anderson 1954).

RESULTS

The light microscope study included material of *Arcytophyllum nitidum*, *A. serpyllaceum*, *Bouvardia ternifolia*, and *Manettia alba* and *M. reclinata*. The first, third, and fifth of these species are the types of their respective genera. Pollen in *Arcytophyllum* and *Bouvardia* show essentially identical spherical, tricolporate pollen with minor variation in the granulation of the exine. Only *Manettia* differs by a sometimes more oblate shape with projecting pores. The grains of *M. reclinata* are commonly lying on their more flattened poles and seem almost triangular. The light microscope also showed prominent raphide bundles in stipules, calyx and sometimes the corolla of *Manettia* that were not seen in *Arcytophyllum* or *Bouvardia* slides.

A review of the genera and species for seed and capsule data is as follows:

Arcytophyllum Willd. ex Schult. in Roem.& Schult., Syst. Veg, Mant. 3:5. 1827.
This Andean and Central American genus of 16 species of shrubs, subshrubs, and suffruticose herbs grows at higher elevations from Costa Rica to Bolivia (Mena 1990). Most species have rather restricted ranges. Mena found the most useful characters to be the shape of the stipules and the leaf and corolla shapes.

We examined seeds of nine of the sixteen species of *Arcytophyllum*, of which six species were treated by SEM. The seeds of the studied species fell into three groups, as outlined below.

Group A

This group includes the type of the genus. The species are *A. filiforme, A. lavarum, A. macbridei, A. muticum, A. nitidum*, and *A. serpyllaceum*. *Arcytophyllum lavarum, A. muticum*, and *A. serpyllaceum* have lenticular seeds, polygonal or suborbicular in outline, with centric punctiform or slightly raised hila (Fig. 1). *Arcytophyllum lavarum* may or may not be winged, but is shown in this figure as being winged. The remaining three species, *A. filiforme, A. macbridei*, and *A. nitidum* were not done by SEM, but their descriptions are included below. Descriptions of the seeds of the six species follow:

Arcytophyllum filiforme (Ruiz & Pav.) Standl.—Seeds 0.7–1.0 mm diam., black, moderately to strongly compressed, suborbicular in outline, lenticular, thickly to thinly concavo-convex, hilar area rounded or slightly raised, areoles not seen in detail. *Harling & Andersson 12638* (US), Ecuador (det. Boom); *Fosberg & Giles 23135* (US), Ecuador (det. L.B.Smith).

Arcytophyllum lavarum K. Schum.—Seeds 0.7–1.0 mm diam., black, strongly compressed, suborbicular or polygonal in outline, lenticular, biconvex, wing absent or partial, very narrow, fragile, hilum punctiform, areoles isodiametric or polygonal, their walls thick, testa smooth. *Cuatrecasas & Leon 26524* (US), Costa Rica, R8a; *Herrera & Robles 791* (US), Costa Rica, B35 (Fig. 2).

Arcytophyllum macbridei Standl.—Seeds 1.4–1.6 mm diam., black, strongly compressed, suborbicular in outline, lenticular, concavo-convex, wing partial, very narrow, fragile, hilum punctiform or slightly raised, areoles not seen in detail. *Wurdack 1273* (US), Peru (dupl.det. Steyermark).

Arcytophyllum muticum (Wedd.) Standl.—Seeds 1.0–1.4 mm diam., black, moderately to strongly compressed, suborbicular or polygonal in outline, lenticular, rather thickly biconvex or only convex dorsally, hilum punctiform, slightly raised, or a short ridge, areoles isodiametric or polygonal, small, their walls thick, testa smooth. *Fosberg 19196* (US), Colombia, (det. Mena), B36; *Haught 5803* (US), Colombia, R7; *Martin & Plowman 93* (US), Colombia (det. Mena) (Fig. 1).

Arcytophyllum nitidum (Kunth) Schltdl.—Seeds 0.7–1.0 mm diam., black, strongly compressed, polygonal to suborbicular in outline, lenticular, convex dorsally, flat or bent ventrally, hilum punctiform, areoles not seen in detail. *Fosberg & St. John 21880* (US), Colombia.

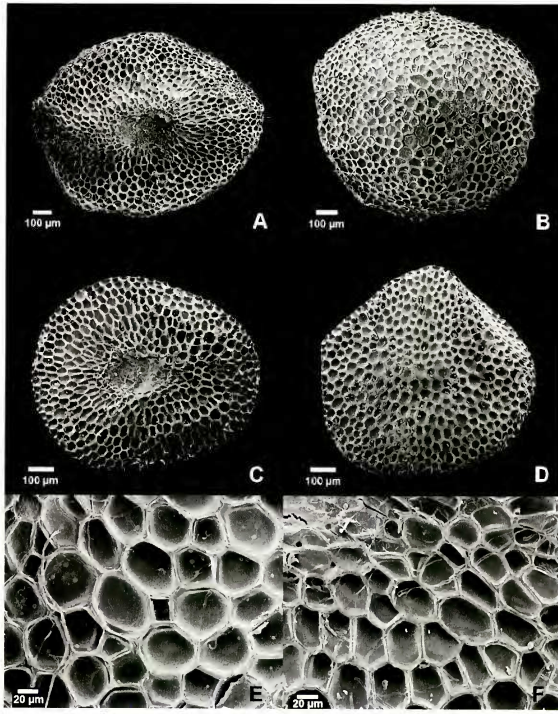

Fig. 1. Seeds of *Arcytophyllum* species examined by SEM. **A, B, E,** *Arcytophyllum muticum*, *Fosberg 19196* (US), Colombia. **C, D, F,** *Arcytophyllum serpyllaceum*, *Williams et al. 22771* (US), Guatemala. **A, C,** ventral views; **B, D,** dorsal views; **E, F,** areoles.

Arcytophyllum serpyllaceum (Schltdl.) Terrell—Seeds 0.6–1.2 mm diam., black, moderately to strongly compressed, suborbicular or polygonal in outline, lenticular, rather thickly biconvex or flat on one face, hilum punctiform, areoles isodiametric or polygonal, small, their walls thick, testa smooth. *Sharp*

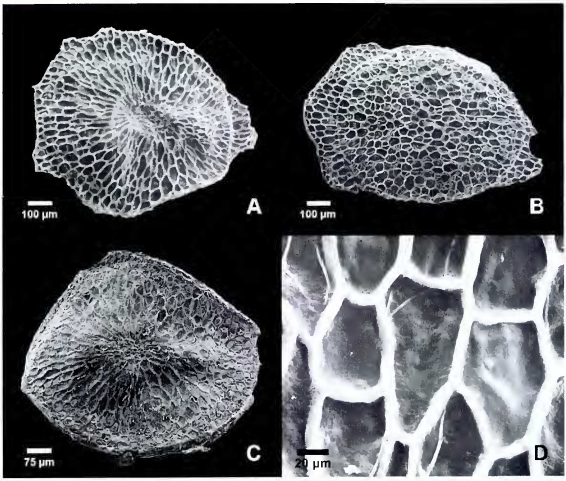

FIG. 2. Seeds of *Arcytophyllum lavarum* examined by SEM. **A, B, D,** *Cuatrecasas & Leon 26524* (US), Costa Rica; **C,** *Herrera & Robles 791* (US), Costa Rica. **A, C,** ventral views; **B,** dorsal view; **D,** areoles.

45143 (TENN), Guatemala, R12; *Williams et al. 22771* (US), Guatemala, B38; *Alexander 1063* (NY), Chiapas, Mexico (Fig. 1).

An inclusive description follows: Seeds 0.6–1.6 mm diameter, black, moderately to strongly compressed, suborbicular or polygonal in outline, thickly to thinly lenticular, faces (sides) flat, concave, convex, or biconvex, wings absent or present, partial, very narrow, fragile, hilum punctiform, rounded, or slightly raised, areoles isodiametric or polygonal, small, walls thick, testa smooth.

Group B

This group includes only *A. aristatum*. Seeds are polygonal in outline, lumpy, not lenticular, and have a strongly raised or ridged ventral face.

Arcytophyllum aristatum Standl.—Seeds 0.7–1.0 mm diam., black, moderately to slightly compressed, lumpy, polygonal in outline, dorsal face convex, ventral face with a strongly raised hilar area or a short to long hilar ridge, areoles small, isodiametric or polygonal, walls thick, testa smooth. *Cuatrecasas*

18976 (US), Colombia; B34; *Lutcyn & Lutcyn 6758* (US), Ecuador; *Steere 8034* (US), Ecuador (Fig. 3).

Group C

This group includes *Arcytophyllum rivetii* and *A. thymifolium* and has elliptical or oblong seeds with a low hilar ridge.

Arcytophyllum rivetii Danguy & Cherm.—Seeds 1.0–1.3 × 0.6–0.7 mm, black, strongly compressed, broadly elliptic or oblong in outline, biconvex, concavo-convex, or flat, wing none or very narrow at one end of seed, hilum a low linear ridge, areoles isodiametric or polygonal, their walls thick, testa smooth. *Wurdack 1288* (US), Peru, B37 (Fig. 3).

Arcytophyllum thymifolium (Ruiz & Pav.) Standl.—Seeds 0.8–1.2 × 0.5–0.7 mm, black or dark brown, strongly compressed, broadly elliptic or oblong in outline, rather thin, concavo-convex or flat, hilum a low linear or oblong ridge, areoles isodiametric or polygonal, their walls thick, testa smooth. *Firmin s.n., 5/12/27* (US), Ecuador, B39; *Fosberg 21196* (US), Colombia; *Schultes & Villarreal 7880* (US), Colombia (Fig. 3).

An inclusive description is as follows: Seeds 0.8–1.3 × 0.5–0.7 mm, black or dark brown, strongly compressed, broadly elliptic or oblong in outline, biconvex, concavo-convex, or flat, wing none or very narrow at one end of seed, hilum a low, linear or oblong ridge, areoles isodiametric or polygonal, their walls thick, testa smooth.

Summary of Arcytophyllum.—A general survey of *Arcytophyllum* seeds shows that they are strongly or moderately dorsiventrally compressed, with a ventral punctiform centric hilum or a hilar ridge. A few species may have very narrow, fragile, partial wings, but the more common state is wingless. The areoles (cells) are usually isodiametric or polygonal and rather thick-walled with smooth testa. There are three distinct kinds of seeds.

Group A seeds are polygonal or suborbicular in outline. The seeds are lenticular, varying thicker or thinner and biconvex or concavo-convex or flat on a face. The hilum is centric, i.e., on or near the center of the ventral face of the seed, and is often punctiform, appearing as a dot or a small round or raised area. (Figs. 1, 2). Group B has thicker, lumpy seeds with ventral face raised or a short to long hilar ridge. (Fig. 3). Group C has oblongoid or ellipsoid seeds which are slightly to strongly concave ventrally. A low narrow hilar ridge extends along part or most of the seed (Fig. 3).

Mena's (1990) description of *Arcytophyllum* seeds as irregularly patelliform (dish- or saucer-shaped) or cymbiform (boat-shaped) and coarsely alveolated (honeycombed) is somewhat misleading because it suggests that they have shallow or deep ventral cavities or concavities such as are typical of *Houstonia* (Terrell 1996). In *Arcytophyllum*, however, the seeds are in Group A lenticular, in Group B lumpy, and in Group C are ellipsoidal or oblongoid and longitudi-

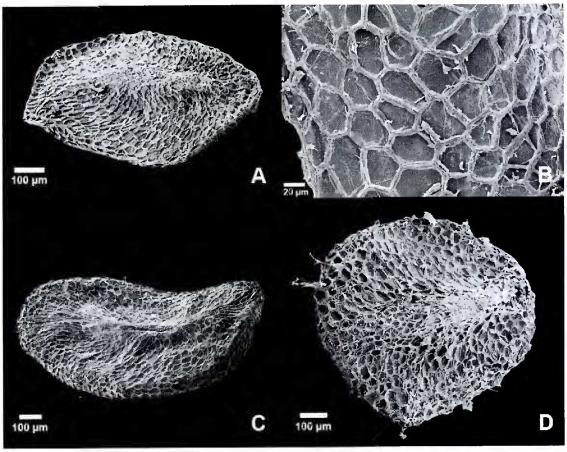

Fig. 3. Seeds of *Arcytophyllum* species examined by SEM. **A–B,** *Arcytophyllum rivetii, Wurdack 1288* (US), Peru. **C,** *Arcytophyllum thymifolium, Firmin s.n.,* 5/12/27, (US), Ecuador. **D,** *Arcytophyllum aristatum, Cuatrecasas 18976* (US), Colombia. **A, C, D,** ventral views; **B,** areoles.

nally concave or bent. The seed surfaces are never honey-combed, but are reticulate and like most seeds of Hedyotideae are made up of walled areoles or cells.

Capsules of *Arcytophyllum* were described by Standley (1921) as biloculate, turbinate to globose, and usually septicidally dehiscent to the base. Mena's description was "septicidal, sometimes only the beginning of the dehiscence loculicidal", crowned by the persistent calyx lobes and intercalycine teeth. For eight of our studied species Mena said that the capsules varied 1–3 mm in diameter, and were mostly subglobose. He found 2–15 seeds per locule (4–30 per capsule). For *A. thymifolium* Mena found 1.7–2 × 2–2.5 mm, which suggests a dimension wider than long. Terrell for *A. thymifolium* recorded 2 × 1 (ellipsoid or oblongoid) in one collection; in a second collection 1.5–2 × 1.0–1.7 (subglobose to oblongoid). Terrell found 5–12 seeds per capsule in *A. lavarum* and *A. thymifolium*. The capsules of *A. serpyllaceum* are 1.5–4 × 2–3.5 mm, turbinate, loculicidal, nerved, and have 8–29 seeds per capsule. This species is further discussed below and compared with *A. muticum*.

Bouvardia Salisbury, Parad. Lond. Pl. 88. 1805.

Blackwell (1968) recognized 31 species in three subgenera in *Bouvardia*. The species are primarily Mexican, with extensions into Central America and southwestern United States, and are shrubs except for four species in the third subgenus. The first subgenus recognized by Blackwell was *Bouvardiastrum* Schltdl. with 15 species, of which we examined *B. capitata*, *B. cordifolia*, *B. laevis*, and *B. multiflora*. The second subgenus, *Bouvardioides* Schltdl. has 8 species, none of which are represented in our study. The third subgenus, *Bouvardia* Schltdl., has 8 species of which we examined *B. ternifolia* and two recently described or transferred perennial herbs, *B. rzedowskii* and *B. xestosperm* (Terrell and Koch 1994), which are similar to and apparently related to the perennial herbs, *B. rosca* Schltdl. and *B. tenuifolia* Standl. Several additional *Bouvardia* species have been described in recent years, but our study utilizes mainly the species studied by Blackwell (1968).

Previous field work in Mexico provided a foundation for the present study. *Bouvardia rzedowskii* was collected and described and *B. xestosperma* was recollected in Oaxaca (Terrell and Koch 1994). Other species of *Bouvardia* were seen in Mexico during this work.

Individual descriptions of seeds are given as follows, with capsule data added from Blackwell (1968). Two groups of species are recognized for this genus.

Group A

The first group includes four shrubby species in subgenus *Bouvardiastrum* (*B. capitata*, *B. cordifolia*, *B. laevis*, *B. multiflora*) and one shrubby species in subg. *Bouvardia* (*B. ternifolia*). These species seem to be generally similar in seed morphology.

Bouvardia capitata Bull.—Seeds 2.5–3.5 mm diam., brown with tan wing, papery thin, orbicular in outline, ventral face concave, seed body 1.0–1.5 mm wide, wing 0.3–1.0 mm wide, its margin entire, undulate, hilum punctiform, often a raised point, areoles radially elongated, their walls thin, testa smooth. *Hinton 8600* (US), Tejupilco, Tepascaltepec (?), Mex. (det. Blackwell), B41 (Fig. 4).

Bouvardia multiflora (Cav.) Schult. & Schult.f.—Seeds 2–3 mm diam., dark brown or black with brown wing, papery thin, orbicular in outline, ventral face concave or almost flat, seed body 0.8–1.4 mm wide, wing 0.2–1.0 mm wide, its margin entire, undulate, hilum punctiform, sometimes a raised point, areoles radially elongated, their walls thin, testa smooth. *H.S. Gentry 8388* (US), Durango, Mexico, (det. Blackwell), B42; *E. Palmer 708* (US), Mexico (Fig. 4).

Bouvardia ternifolia (Cav.) Schltdl.—Seeds 2–3 mm diam., black with brown wing, papery thin, orbicular in outline, ventral face concave, seed body 1.0–2.2 mm wide, wing 0.2–0.6 mm wide, its margin entire, undulate, hilum punctiform, a slightly raised point or rounded area, areoles radially elongated, their walls thin, testa smooth. *Dziekanowski et al. 1860* (US), Hidalgo, Mexico, H52 (Fig. 4).

An inclusive description is as follows: Seeds 2–3.5 mm diam., brown, black,

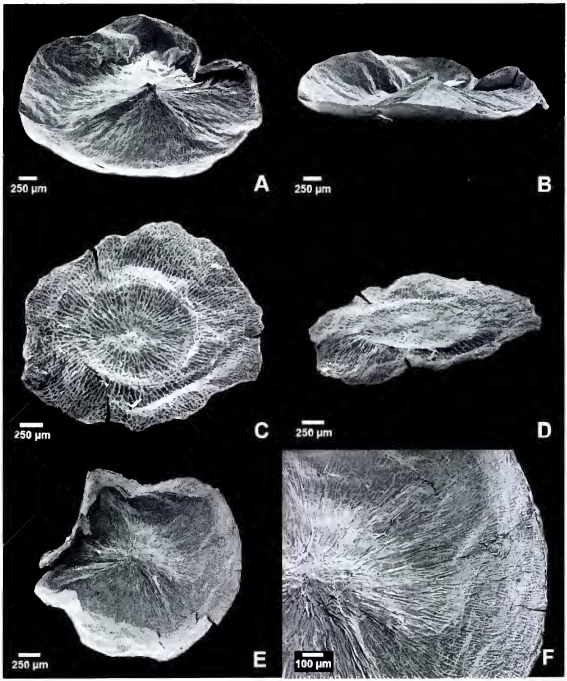

FIG. 4. Seeds of *Bouvardia* species examined by SEM. **A–B**, *Bouvardia capitata, Hinton 8600* (US), Mexico. **C, D**, *Bouvardia ternifolia, Dziekanavski et al. 1860* (US), Mexico. **E, F**, *Bouvardia multiflora, H.S. Gentry 8388* (US), Mexico. **A–F**, ventral views; **F**, enlarged section showing areoles.

or tan, papery thin, orbicular in outline, ventral face concave, seed body 0.8–2.2 mm wide, wing 0.2–1.0 mm wide, its margin entire, undulate, hilum punctiform, a raised point or rounded area, areoles radially elongated, their walls thin, testa smooth.

Capsules in group A have the following inclusive description: 3–9 × 3.5–11

mm., subglobose or slightly oblate, dehiscing loculicidally then septicidally (Blackwell). Standley (1921) recorded capsules as globose and loculicidally dehiscent.

Group B.

The second group includes two recently described or transferred perennial herbs in subg. *Bouvardia* (*B. rzedowskii* and *B. xestosperma*).

Bouvardia rzedowskii Terrell & S.D. Koch—Seeds 1–2 mm diam., dark brown with brown wing, papery thin, orbicular in outline, ventral face concave or flat, seed body 0.5–1.0 mm wide, wing 0.1–0.4 mm wide, its margin entire, undulate, hilum punctiform, sometimes a raised point, areoles radially elongated, their walls thin, testa smooth. *Koch & Koch 8935* (CHAPA), Oaxaca, Mexico, H51 (Fig. 5).

Bouvardia xestosperma (Rob. & Greenm.) Terrell & S.D. Koch—Seeds 1–2 mm diam., dark brown or black, thin, orbicular or oval in outline, ventral face flat or slightly concave, seed body 0.3–1.0 mm wide, wing partial or complete, 0.1–0.5 mm wide, entire, sometimes undulate, hilum punctiform, a slightly raised point, areoles radially elongated, their walls thin, testa smooth. *Koch & Koch 8934* (CHAPA), Oaxaca, Mexico, B45; *Conzatti & Gonzalez 248* (GH), Oaxaca, Mexico, H4 (Fig. 5).

Inclusive description: Seeds 1–2 mm diam., dark brown or black, papery thin, orbicular or oval in outline, ventral face concave or flat, seed body 0.3–1.0 mm wide, wing partial or complete, 0.1–0.5 mm wide, entire, undulate, hilum punctiform, sometimes a raised point, areoles radially elongated, their walls thin, testa smooth.

Capsules 3–5 × 3.5–4.5 mm in *B. rzedowskii*, and 2.5–4 mm long in *B. xestosperma*, with loculicidal dehiscence.(Terrell & Koch 1994).

Due to limited sampling summaries are not given for *Bouvardia* and *Manettia*; however, a comparison of *Bouvardia* groups A and B shows that group B of perennial herbs has smaller seeds and partial instead of complete wings. *Bouvardia ternifolia*, a shrubby species, seems more allied to *Bouvardiastrum* or *Bouvardioides* which have shrubby species.

Manettia Mutis ex L., Mant. Pl. 553, 558.1771, nom. cons.

The genus includes vines or herbs distributed in tropical America, principally in South America. Standley (1921) treated 10 species from West Indies, Mexico, and Central America. Chung (1967, 1968) studied five species in the section *Heterochlora* K. Schum. and six species in section *Pyrrhanthos* K. Schum. Steyermark (1974) estimated 140 species of *Manettia* altogether, and treated 19 species from Venezuela. *Manettia* has broadly winged seeds similar to those of *Bouvardia*. Our data on *Manettia* are limited, and our main purpose here is to present seed descriptions of five species and SEM illustrations of three species of *Manettia* for comparison with similarly-seeded *Bouvardia*. We do not reach any conclusions regarding possible relationships to *Bouvardia*.

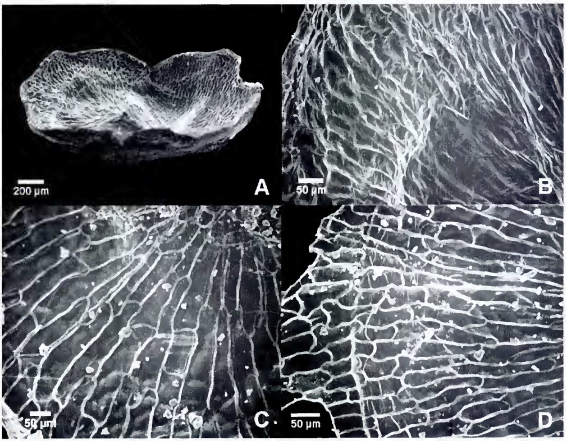

FIG. 5. Seeds of *Bouvardia* species examined by SEM. **A–B,** *Bouvardia rzedowskii, Koch & Koch 8935* (CHAPA), Mexico. **C, D,** *Bouvardia xestosperma, Conzotti & Gonzalez 248* (GH), Mexico. **A,** ventral view; **B, C, D,** areoles.

We examined the seeds of the following five species of *Manettia*: *M. calycosa* var. *karsteniana*; *M. divaricata*; *M. flexilis*; *M. meridensis*, and *M. reclinata*. Three of these were examined by SEM: *M. calycosa* var. *karsteniana*, *M. flexilis*, and *M. reclinata*.

Manettia calycosa Griseb.var. *karsteniana* K. Schum.—Seeds 0.8–1.1 mm diam., black with brown wing, thin, orbicular in outline, flat or slightly concave ventrally, seed body ca. 0.7 mm wide, wing 0.1–0.3 mm wide, its margin erose, hilum punctiform, areoles radially elongated, walls thin, testa smooth. *Steyermark & Wiehler 106576* (US), Venezuela, B47 (Fig. 6).

Manettia divaricata Wernham—Seeds 2–3 mm diam., black with brown wing, thin, orbicular in outline, flat or slightly concave ventrally, seed body 1.0–1.5 mm wide, wing 0.4–1.0 mm wide, its margin ornately erose or toothed, hilum depressed to slightly raised, areoles not seen in detail. *Schunke V. 838* (US), Peru, (det. D.R. Simpson).

Manettia flexilis Brand.—Seeds 2.0–3.5 mm diam., dark brown with light brown wing, thin, orbicular in outline, flat, seed body 0.6–1.5 mm wide, wing 0.4–1.2 mm wide, its margin erose, hilum punctiform or flat, areoles radially

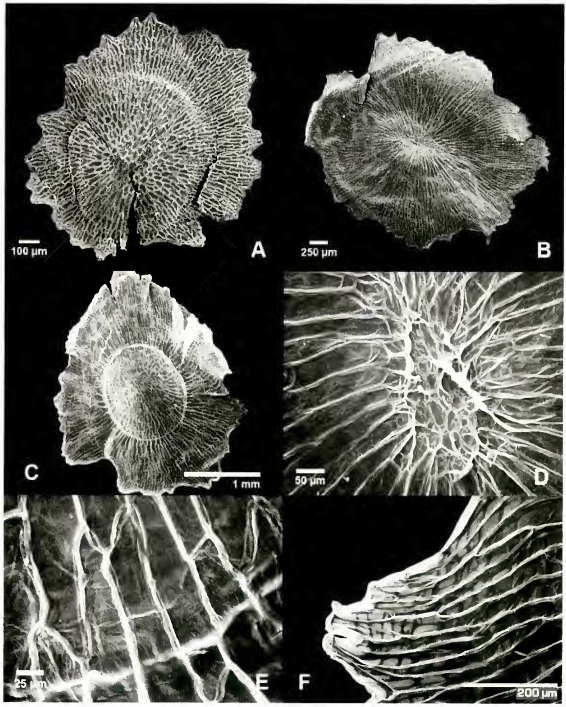

Fig. 6. Seeds of *Manettia* species examined by SEM. **A,** *Manettia calycosa* var. *karsteniana, Steyermark & Wichler 106576* (US), Venezuela. **B,** *Manettia reclinata, Hoover 161* (US), Mexico. **C–F,** *Manettia flexilis, Smith P2360* (US), Costa Rica. **A–B,** ventral views; **C,** dorsal view; **D,** hilar area; **E, F,** areoles and wing areoles.

elongated, walls thin, testa smooth. *A. Smith P2360* (US), Costa Rica, H32, (det. S. F. Blake) (Fig. 6).

Manettia meridensis K. Schum.—Seeds 2–3 mm diam., black with dark brown wing, thin, orbicular in outline, flat or slightly concave ventrally, seed

body 0.5–1.5 mm wide, wing 0.4–0.8 mm wide, its margin entire or minutely erose, hilum punctiform, flat or a slightly raised point, areoles not seen in detail. *Bro. Daniel 1707* (US), Colombia.

Manettia reclinata Mutis ex L.—Seeds 2.5–3.0 mm diam., black with brown wing, thin, orbicular in outline, flat or slightly concave ventrally, seed body 0.7–1.2 mm wide, wing 0.5–1.2 mm, its margin erose, hilum area flat or slightly depressed, areoles radially elongated, walls thin, testa smooth. *Hoover 161* (US), Chiapas, Mexico, B46 (Fig. 6).

Inclusive description of the five species is as follows: Seeds 0.8–3.5 mm diam., black or brown, thin, orbicular in outline, flat or slightly concave ventrally, seed body 0.5–1.5 mm wide, wing 0.1–1.2 mm wide, its margin erose, coarsely toothed, or entire, hilum punctiform, flat or depressed, or slightly raised, areoles radially elongated, walls thin, testa smooth.

Seeds of *Manettia* have wings with margins erose or coarsely and irregularly toothed, much more ornate than *Bouvardia* wings.

Manettia capsules were described by Standley (1921) as septicidally dehiscent, obovoid or turbinate, and coriaceus or chartaceous. Steyermark (1974) also considered the capsules as septicidally dehiscent and described *M. calycosa* as subglobose to ellipsoid or turbinate and 4–7 mm long; for *M. reclinata* obconic and 10–12 × 7–9 mm.

In this study we found *M. divaricata* with capsules 10 × 5.5 and obovoid; *M. meridensis* 5 × 5 and obovoid; and *M. reclinata* 8 × 6.5–8 mm wide and subglobose or broadly ellipsoid. All capsules seen had septicidal dehiscence. Capsules often had two separated halves with each half having a slit or longitudinal opening into the locule reminescent of the diplophragmous capsules of *Hedyotis* subgenus *Hedyotis* (Terrell & Robinson 2003).

DISCUSSION

Capsule characters Capsules in *Arcytophyllum* and *Manettia* have septicidal dehiscence, whereas *Bouvardia* primarily has loculicidal dehiscence followed by septicidal dehiscence. Capsule thicknesses and sizes are much greater in *Bouvardia* and *Manettia* and more varied in shape, although a predominant shape in *Arcytophyllum* and *Bouvardia* is subglobose.

Seed characters The following descriptive key is based on the the present sample of species. *Bouvardia* and *Manettia* seeds are so similar that they are here treated as one unit.

1. Seeds 0.6–1.6 mm long or diam, orbicular or elliptical in outline, moderately or strongly compressed, lenticular, faces biconvex, concavo-convex, or flat or else somewhat concavo-convex, wings none or very narrow and partial, hila centric, flat or slightly depressed or slightly raised, or else a low ridge, areoles isodiametric or somewhat polygonal, their walls thick _____ **Arcytophyllum**
1. Seeds 0.8–3.5 mm diam, orbicular in outline, strongly compressed, flat, thin, most

species broadly winged, wing papery, fragile, seed body and wing often incurved or concave; wing margin entire and undulate (*Bouvardia*) or erose or toothed (*Manettia*), or else wing narrow, hila centric, flat or sometimes raised slightly to form a point, areoles radially elongated, their walls thin _____ **Bouvardia, Manettia**

Relationships of Arcytophyllum serpyllaceum

The species long known as *Hedyotis serpyllacea* Schltdl. (Linnaea 9:599. 1834) occurs at higher elevations (usually 1500-3500 m) in southern Mexico (Veracruz, Chiapas, Oaxaca) and Guatemala. It is a prostrate, creeping, mat-forming, suffruticose herb that is often abundant in open, grassy places or fields. It produces small white flowers that tend to be purplish or greenish on their abaxial faces. During field work in Mexico (Terrell & Koch 1994) the species was observed and collected in Veracruz.

This species was long retained in *Hedyotis* but differed from other Mexican species that had been placed in that genus. Terrell (1999) described and discussed it in detail, transferred the name *Hedyotis serpyllacea* to *Arcytophyllum* (1827) and noted that there is a precedent for its placement in *Arcytophyllum*. John Donnell Smith (1893) described the species from Guatemala, placing it in *Mallostoma* (Karst. 1862), a synonym of *Arcytophyllum*, as *M. shannoni*. Smith provided a rather complete description of the entire plants, including the following: "capsule obovate ... 8-costate, loculicidal at apex, septicidal at base; seeds 8-20, compressed, roundish, ... finely punctate, black and shining." The "punctate" seed description apparently refers to the polygonal areoles, visible at lower power magnification as reticulations, a common feature of hedyotoid seeds. Standley (1916) transferred *M. shannoni* (without comment) to *Arcytophyllum* as *A. shannoni*, but included only *A. lavarum* in his treatment of Rubiaceae for the North American Flora (Standley 1921). (Apparently, *A. muticum* was not known from Panama and Costa Rica in 1921; see other comments below about *A. muticum*)

Although Mena (1990) in his revision of *Arcytophyllum* had merely listed *Hedyotis serpyllacea* in his category of Excluded and Dubious Names, nonetheless there are similarities to the prostrate, suffruticose species of *Arcytophyllum*, suggesting that *A. serpyllaceum* could be an extension of *Arcytophyllum* northward from Costa Rica into Guatemala and southern Mexico.

The transfer of this species to *Arcytophyllum* was questioned by Andersson et al. (2002) based on their Analysis 1, data from the *rps*16 intron. A phylogenetic tree indicated a close relationship to *Bouvardia* rather than *Arcytophyllum*. Their study of *A. serpyllaceum* was based on a Mexican collection from the MO herbarium, *Stafford et al. 203*. Hoping to examine this collection we corresponded with Charlotte Taylor, curator of Rubiaceae at MO. She has been unable to find this herbarium sheet either under *Hedyotis* or related genera, although Andersson has written to Terrell stating that the loan of MO specimens to GB was returned to MO. Presently, the location of this specimen remains unknown.

TABLE 1. Comparison of characters of *Arcytophyllum muticum* and *A. serpyllaceum*.

Characters	muticum	serpyllaceum
Roots and stems	"Subshrubs," prostrate, stoloniferous, mat-forming	Suffruticose herbs, prostrate, woody rhizomes, creeping, mat-forming
Stipules	Genus: interpetiolar, entire or with toothed projections, glabrous or with pustuliform papillae Species: Decurrent, deltate, with acuminate projections 0.4–0.7 mm long, scattered short hairs	Interpetiolar, to 2 mm long, ovate, with short to long narrow caudae, marginal teeth with apical glands, glabrous to ciliolate
Leaves	Sessile or subsessile, 2.5–4.5 × 0.8–1.8 mm, ovate, transversely falcate, coriaceous, glabrous	Sessile, 2–9 × 1–5 mm, ovate or elliptic, thickened, coriaceous, glabrous
Flowers	Solitary, sessile, apparently isostylous	Solitary, pedicels to 7 mm long, heterostylous
Calyces	1–2.5 mm long, trullate or triangular, glabrous, with intercalycine teeth	Lobes (1–)3–8 × 0.5–1.5 mm, lanceolate to ovate or obovate, glabrous, with intercalycine teeth
Corollas	6–9 mm long, salverform–funnelform, purple or bluish abaxially, white adaxially	(4–)6–10 mm long, funnelform, greenish or purple abaxially, white adaxially, thickish
Corolla lobes	2–4.5 × 2–3.5 mm, deltate, papillose, scattered hairs in margin and abaxially, scattered shiny scales adaxially	2.5–4.8 × 1.2–1.7 mm, ovate or elliptic, densely white pubescent adaxially
Corolla tubes	3–4.5 × 1–2 mm, glabrous	3–5 × 2–3 (at throat), glabrous abaxially, pubescent distally adaxially
Stamens	Anthers 1 × 0.3 mm, slightly exserted	Anthers ca. 1–2 mm long, oblong, slightly exserted (thrum flowers), included (pin flowers)
Stigmas	1 mm long, papillose adaxially	1–2.3 mm long (pin), 1–1.4 mm long (thrum)
Capsules	1–3 mm diam., globose, septicidal, 4–24 seeds/capsule	1.5–4 × 2–3.5 mm, broadly oblong or obovate, loculicidal, 8–29 seeds/capsule
Seeds	1.0–1.4 mm diam., often strongly compressed, often polygonal in outline, lenticular, often biconvex, hilum sl. raised, areoles often isodiametric, small.	0.6–1.2 mm diam., other characters very similar to those of *A. muticum*

In the absence of confirmation of the voucher for the study by Andersson et al. (2002), the present study follows the species placement based on structural features of the plants. Two species of *Arcytophyllum* occur in Central America and are of particular interest here. These are *A. lavarum*, endemic to Costa Rica and Panama, and *A. muticum*, native to Costa Rica and Panama and extending south to Ecuador. (Mena 1990 does not list *A. muticum* from Costa Rica except as the type for a synonym, but there are nine collections from Costa Rica in herbarium US). The two similar species, *A. muticum* and *A. serpyllaceum*, are compared in Table 1, listing all of the main characters. The flowers of the two species differ in styly, but this is not considered a generic difference (e.g., Terrell 1996 found both stylies in *Houstonia*).

The data on capsules suggest that *A. muticum* differs somewhat in size, shape, and number of seeds per locule (Table 1) from *A. serpyllaceum*. The two species differ also in *A. muticum* having septicidal dehiscence versus loculicidal dehiscence in *A. serpyllaceum*. Comparison of dehiscence in other genera of Hedyotideae shows considerable variation and the presence of septicidal (e.g., *Hedyotis* subg. *Hedyotis*) and loculicidal dehiscence (e.g., *Houstonia* and *Oldenlandia*).

Contrary to statements by Andersson et al. (2002) that *A. serpyllaceum* seeds resemble those of *Bouvardia*, we find that their seeds are distinctly different, not only in the presence or absence of conspicuous or inconspicuous wings, but also in the appearance of the often raised pointed hila and in the presence of thick-walled isodiametric areoles versus thin-walled radially elongate areoles.

Comparison of seeds of *A. muticum* and *A. serpyllaceum* show them to be so similar that we did not detect any differences in shape, position of hilum, or sizes and shapes of the areoles, and without identity data it would be impossible to distinguish them (Fig. 1). *Arcytophyllum lavarum* was also similar to the other two species (Fig. 2).

A more detailed study of additional species of Hedyotideae is needed in order to provide both molecular and morphological evidence concerning relationships. It is hoped that time will permit such a survey to be carried out with assistance from a person knowledgeable in molecular studies.

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